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OLIGOCHAETA

.

PART I. MICRODRILI (mainly ENCHYTRAEIDAE)

Ву

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By J. Stephenson, M.B., D.Sc., F.R.S.

(Text-figs. 1–14)

INTRODUCTION

THE Microdrili in the present collection have been obtained from four localities: the Palmer Archipelago, almost directly south of Cape Horn, near Graham Land, between 64° and 65° S lat.; the South Orkneys, between Graham Land and South Georgia, in S lat. 60–61°; South Georgia, approximately in S lat. 54–55° and W long. 38°; and Gough Island, in the middle of the South Atlantic, somewhat to the south-east of Tristan d'Acunha, in S lat. 40°. These places are more or less in line with each other, the line stretching from south-west to north-east, from the Palmer Archipelago to Gough Island; but Gough Island is at a considerably greater distance from the other localities than these are from each other.

Apparently no Microdrili have previously been collected in the Palmer Archipelago, the South Orkneys, or on Gough Island; but from South Georgia we possess the records of Michaelsen (1888) and Michaelsen (1905) (Hesperodrilus crozeteusis, Rhyacodrilus coccineus, Marionina georgiana, M. exigua, Lumbricillus maximus, Enchytraeus albidus, Michaelsena monochaeta). While Marionina exigua, Rhyacodrilus coccineus, and (apparently) Hesperodrilus crozetensis have not been recovered by the present expedition, the tubes from South Georgia contain the other species previously found there, and in addition Marionina aestuum, sp.n., Lumbricillus autarcticus, sp.n., L. macquariensis (known previously from the sub-Antarctic islands of New Zealand), Enchytraeus australis, sp.n., E. colpites, sp.n., a probably undescribed species of Hesperodrilus, and an indeterminable specimen belonging to the genus Achaeta.

My best thanks are due to the authorities of the British Museum (Natural History), where my investigations were carried out, for the facilities so kindly afforded me. All the specimens, including types of the new species, are now in the Museum.

GEOGRAPHICAL DISTRIBUTION

The facts of distribution of the earthworms (Megadrili) of the sub-Antarctic islands are of interest as contributing to a discussion of the problem of an Antarctic Continent and its former connections as a factor in zoogeography. The problem has been argued, principally by Michaelsen and Benham, on the basis of the present-day distribution of the acanthodriline genus *Microscolex*; and I have recently (Stephenson, 1930) given an outline of their arguments, with references to their papers. Briefly, Benham sees the

present distribution of species of *Microscolex* in southern and sub-Antarctic islands, from the South American eastwards to the New Zealand region, as a result of the former existence of an Antarctic Continent with a temperate climate, with northward extensions which reached and included the scattered islands of the southern seas; while Michaelsen looks on this distribution as due to the dispersal across the ocean of the genus *Microscolex* (of which at least some species are littoral in habitat and euryhaline) from its home in the south of South America by the agency of the "west wind drift".

But it is generally recognized that the distribution of the smaller Oligochaeta (Microdrili), and especially of the freshwater and littoral genera, has little bearing on the larger questions of zoogeography. They are easily transported by human or other agency or by the inanimate forces of nature; and accordingly we see, for example, *Enchytraeus albidus*, one of the commonest worms of Europe, widely distributed in the islands of the southern seas (though apparently absent from the warmer regions of the globe). It is therefore mainly for the simple purpose of completing our survey that I add here the following notes on distribution.

Of the worms brought back by the present expedition Marionina grisea, M. aestuum, Lumbricillus antarcticus, Enchytraeus colpites, and Michaelsena monochaeta have each been found only in a single locality (M. monochaeta in the same locality also by a previous expedition).

The genus *Hesperodrilus* (fam. Phreodrilidae), represented in the present collection by an example from South Georgia which is specifically indeterminable, is known from Tierra del Fuego, South Chile, South Georgia, the Crozets, Kerguelen Island, Campbell Island, New Zealand, and New South Wales.

The genus *Achaeta* (this and the following genera belong to the Enchytraeidae), of which an indeterminable example was taken in South Georgia, is also known from Europe and New Zealand.

Marionina grisea and M. aestuum, though I consider them as specifically distinct, form with M. werthi and M. benhami (cf. p. 250) a closely interrelated group, the species of which stretch in a line from the Palmer Archipelago (grisea) through South Georgia (aestnum) and Kerguelen (werthi) to Macquarie Island in the New Zealand region (benhami), half-way round the globe.

Marionina georgiana has been found, by the present or by previous expeditions, in South Georgia, the Falkland Islands, and the Crozets.

Lumbricillus lineatus (a common European species) in the Palmer Archipelago, the South Orkneys (between the last-mentioned locality and the next), and (with some element of doubt) South Georgia, as well as in Tierra del Fuego.

L. maximus in the Palmer Archipelago, the South Orkneys, South Georgia, the Crozets, and (var. Robinson) New Amsterdam Island, in the South of the Indian Ocean.

L. macquariensis in South Georgia and in the New Zealand region (Macquarie, Auckland, and Campbell Islands), but not hitherto in any of the islands between.

Enchytraeus albidus (common in the northern hemisphere) in Southern Patagonia,

Tierra del Fuego, the Falkland Islands, South Georgia, Kerguelen, the Crozets, and the southern islands of the New Zealand region.

E. australis in South Georgia and Gough Island (in mid-Atlantic, not far from Tristan d'Acunha).

All the above genera of Enchytraeidae are known from Europe, and *Marionina*, *Lumbricillus*, and *Enchytraeus*, which are among the commonest representatives of the family, from North America also.

Though *Rhyacodrilus coccineus* (Tubificidae), recorded from South Georgia by Michaelsen (1905), was not obtained by the present expedition, it is interesting to note that it occurs in Europe, in the Crozets (Michaelsen, 1905 *a*), and in New Zealand (= *Taupodrilus simplex*, Benham, 1903).

Though the above presentation contains some rather striking facts, such as the occurrence of *Lumbricillus macquariensis* only in the widely separated localities of South Georgia and the southern islands of the New Zealand region, and similarly of *Enchytraeus australis* only in South Georgia and Gough Island, it can, owing to the ease with which these worms or their cocoons can be transported, hardly be said to contribute data of much value for zoogeographical discussion. We cannot rule out transport by human agency or by natural forces; though, of course, while the facts give no support to the view of a recent temperate Antarctica as a factor in zoological distribution, they are at least not against it.

DEGENERATION OF THE INTERNAL ORGANS IN THE ENCHYTRAEIDAE

In a number of the worms in the present collection the task of identification and description was rendered difficult or even (as in the specimen belonging to the genus *Achaeta*) impossible by a marked degeneration of the interior of the animal.

This condition was very common in the numerous specimens of *Lumbricillus maximus*, the most abundantly represented species in the collection; in most of the batches some, it might be even all, of the worms showed the change. In the body wall the muscular layers were breaking up, the longitudinal muscle coat was losing its continuity and its cohesion, small lengths of muscle fibres were being shed and a number of such fragments were loose in the anterior segments, where they were apparently becoming converted into a homogeneous somewhat waxy-looking substance. Some of the lymph corpuscles were vacuolated, and many were disintegrating.

The alimentary canal shows the degenerative changes in a very marked degree. The pharynx breaks up with the formation of vacuolar spaces, and the setting free of small round or irregular cells and non-nucleated fragments. The cells of the alimentary epithelium are shed into the cavity; in the preclitellar segments the oesophagus is seen to have lost the whole of its epithelial lining, and its lumen is full of small irregular cells and granular debris; behind segment 14 there is a regular epithelial layer, which here and there is becoming detached but is still continuous.

The chloragogen cells become greatly elongated, more than 100μ high, and vacuolated, the vacuoles constituting the greater part of the cell, and arranged either in a single series along its length or in more than one series.

In the spermathecae the epithelium is shed as a still more or less connected layer, the wall of the organ being reduced to a thin membrane.

In the final stages of degeneration the external annulation is lost, and in the worms cleared for microscopic examination no internal structure is visible, except that sometimes the alimentary canal is still distinguishable, with some of the ova, and traces of the spermathecae.

Among the specimens of *Marionina georgiana*, the only one which was fully mature was not degenerate, and was well preserved in every way. Another example, only in the early stage of sexual maturity, with none of the sexual organs fully formed, showed changes in the alimentary canal—the intestinal epithelium behind the clitellum was loosening itself from the substratum and beginning to disintegrate; in the body-wall the muscular layer had for the most part become homogeneous and waxy-looking; and a dense fibrous coagulum was seen in places in the body-cavity, applied to the chloragogen layer of the gut.

In the specimens of *Michaelsena monochaeta* I found the genital segments and those behind them in a curious condition. There was little free space in the segments, which were filled by a mass of cells and cell degenerations, but with no free spermatozoa or stainable male cells at any stage, and no ova; this filling out with degenerating masses was continued backwards to segment 20, beyond which my sections did not go. In a specimen in which this condition was carried to an extreme, it was noted that the alimentary canal was not much altered, the heavy ciliation of the lining epithelium being preserved.

The single example of the genus *Achaeta* was much disorganized internally; both the alimentary canal and the interior of the genital segments were in a very degenerate state.

The appearances described above do not seem to be due to bad fixation; the specimens of *Lumbricillus maximus*, in which degeneration is most frequent, have been fixed with great care, so as to preserve them in an extended condition, which naturally greatly facilitates examination and sectioning; indeed the same holds for most of the worms in the collection. Speaking generally, even if small worms such as these Enchytraeids were merely thrown promiscuously into spirit, we should get sections which were perfectly usable for morphological purposes (though the worms would doubtless be very inconveniently bent and twisted). Moreover, some specimens of a batch may be degenerate, others not so (e.g. in the case of *Marionina georgiana*). The only supposition by which bad fixation could be held responsible for the appearances would be that the worms were already dead and beginning to disintegrate before being taken for fixation; but this I am sure we can exclude.

I have previously recorded (1926) a not very dissimilar degenerative phenomenon in Enchytraeids, and curiously, there also in worms from a frigid region—Arctic, however, not Antarctic (Spitsbergen). In them I frequently found a wholesale degeneration and shedding of the alimentary epithelium, sometimes with overgrowth of the chloragogen

layer (compare the description of *Lumbricillus maximus* above). I was there inclined to ascribe the appearances to excessive parasitization of the alimentary canal, though I had to confess that in some specimens of extreme degeneration there was no evident parasitization.

Yet more recently I have again come across examples of degeneration in Enchytraeids; some small worms belonging to the genus *Lumbricillus* sent to me from Plymouth by Mr J. S. Colman proved to be specifically indeterminable, owing to a wholesale degeneration of the organs—not the genital organs only, nor the alimentary canal only. Specimens that I have since received from Mr Colman, at a different time of the year, have given me no trouble, and I hope shortly to describe them as a new species, *L. pumilio.* I think the condition here is probably a post-maturity degeneration (*v. infra*)—which, however, has spread beyond the genital organs and affected the whole body.

Mrázek (1910) found that after keeping for some time in unfavourable conditions, Tubificids showed in the coelomic cavity what he took to be portions of the longitudinal muscular layer, sometimes in large amount, so that the coelom was full of this material; the fragments are sometimes engulfed by the amoebocytes of the cavity. The genital organs were degenerating at the same time, but Mrázek does not connect the two degenerations.

I might also recall the fact that in the Naididae there is sometimes a degeneration of the alimentary tract at the height of sexual maturity (in the genera *Nais*, *Dero*, *Haemonais*; cf. Stephenson, 1930, p. 131, and references there); but in these worms the other organs are intact.

I think my first acquaintance with these degenerations was many years ago, when I was working in India, and received from Burma, through the Indian Museum, a number of Enchytraeids which had been found attacking rice, burying themselves in and living in the shoots; an identification was therefore of some economic interest. However, I was unable to say anything, except to make a request for more material, taken, if possible, at a different time of the year. I subsequently received a second consignment; but here again the same condition was present, and I was unable to do anything with it. I have no doubt that the Agricultural Department, which sent the worms, thought I was a particularly incompetent worker.

That the genital organs of Oligochaetes undergo regression after the period of sexual maturity is well known; the changes include the production of large numbers of phagocytes, and the disappearance of the sexual organs by phagocytosis. That the spermatozoa remaining in the seminal vesicles or free in the testicular segments are ingested by phagocytes is familiar to us mainly from the work of Cognetti (1911, 1930) and Černosvitov (1930); for an account of the histological changes in the degenerating organs, and their disappearance by phagocytosis, we are dependent on Černosvitov (1930 a), who describes these processes in *Tubifex*.

To which of these forms of degeneration the phenomena described in the present paper are to be assimilated it is difficult to say. They can here hardly be due to parasiti-

zation; parasites (Anoplophryina) are not uncommon in the alimentary canal of these worms, but they do not occur in any extraordinary numbers, and the degree of parasitization would pass without comment if found in specimens of Enchytraeids from our own shores.

Are all the above-mentioned forms of degeneration at bottom one—a form which comes on at the end of life, which is sometimes introduced by (or is an extension of) the normal post-maturity degeneration of the genital organs, sometimes by the changes in the alimentary canal?

VARIATION IN FORM OF THE NEPHRIDIA IN THE ENCHYTRAEIDAE

In seeking for characters on which to base specific distinctions in the Enchytraeidae the form of the nephridia has been much used—e.g. the size of the anteseptal portion of the organ, which may consist of the funnel only, or may comprise more or less of the glandular part in addition; the shape of the postseptal; the length of the duct relatively to that of the postseptal; its direction—downwards, forwards, or backwards; and especially the place of origin of the duct—at the hinder end, or from some place on the under surface nearer or further from the hinder end.

I have previously (1922) drawn attention to the variability of some of these characters; and the following notes, made in the course of examining the sections (all longitudinal) of some of these worms, seem to confirm what I then wrote. The only really fixed feature of the nephridia seems to be the size of the anteseptal relatively to that of the postseptal portion.

In a specimen of *Lumbricillus maximus*, in one organ the duct left the hinder end of the postseptal and passed backwards and then downwards to the surface; in a neighbouring segment the duct left the under surface of the postseptal some distance in front of the hinder end, passing thence first forwards and then downwards and backwards. Similar variations in the place of origin of the duct are found in *Mariouina aestuum* (see the description of this worm, *post*).

In *Enchytraeus albidus*, in consecutive preclitellar segments, the nephridial duct was seen in one to come off at the middle of the length of the nephridium, in the other from the hinder end; in other preclitellar segments it came off from the under surface in front of the hinder end—about one-third of the length of the postseptal from the hinder end; while behind the clitellum it left the postseptal at the posterior end. The duct may pass backwards, backwards and downwards, nearly directly downwards, or downwards and forwards, all in four consecutive segments.

The shape of the postseptal, as seen in sections, depends on the direction in which it is cut. It seems (in *L. maximus*) to be considerably flattened from above downwards, and hence appears broadly oval in a more or less frontal series, narrow and elongated in a sagittal series.

SYSTEMATIC

Family PHREODRILIDAE

Genus Hesperodrilus, Bedd. em. Michaelsen

Hesperodrilus, sp. incert.

St. WS 62. 19. i. 27. Wilson Harbour, South Georgia. From haul labelled "Moss dwellers" (so on the label; in the Station List WS 62 is said to consist of two hauls, from 15-45 and 26-83 m. respectively). A single specimen, not fully mature; along with five specimens of *Lumbricillus antarcticus*.

I am unable to identify the specimen; it seems, however, to be specifically distinct from *H. crozetensis*, recorded from South Georgia by Michaelsen (1905).

Family ENCHYTRAEIDAE

Genus Marionina, Michaelsen

Marionina georgiana (Michaelsen) (Figs. 1-3).

Pachydrilus georgianus, Michaelsen, 1888, p. 65, pl. ii, figs. 7 a, 7 b. Marionina georgiana, Michaelsen, 1905, p. 5. Marionina georgiana, Michaelsen, 1905 a, p. 15, pl. i, fig. 2. Marionina georgiana, Baylis, 1916, p. 298.

St. MS 71. 9. iii. 26. From moss between Grytviken and Maiviken, East Cumberland Bay, South Georgia. Six specimens, mostly non-sexual or in early sexual stage, one fully mature; along with a single specimen of the genus *Achaeta*.

Michaelsen largely supplemented his original account (1888) by the examination of specimens from the Crozets (1905 a). The species appears to be somewhat variable, and the following notes may add to our knowledge.

Length 5–7 mm.; diameter 0.3-0.35 mm., up to 0.4 mm. at the clitellum. Segments 37, 38, 32 (? complete), 30 (? complete), 27 (apparently complete).

The setae are slightly lumbricilline in shape (i.e. with a slight double curve). The ventral bundles contain (3) 4, 5 (6) in front of the clitellum, and (2) 3, 4 behind; the lateral bundles have 2-4 setae both in front of and behind the clitellum.

The clitellum, occupying segments xii-xiii, is very slightly marked, and is wanting altogether ventrally.

Postpharyngeal bulbs are present (for a discussion of these structures cf. Stephenson, 1922 a, or for a short general description, Stephenson, 1930).

The dorsal vessel begins as a considerable swelling in segment xii.

The anteseptal portion of the nephridium is small, but not very small; it includes more than merely the funnel, and is about half as long as the postseptal; the duct is continued backwards and then downwards from the hinder end of the organ.

The cerebral ganglion is shown in Fig. 1; the shape scarcely agrees with that shown by Michaelsen in his original account, being narrower in the middle and broader behind, with the posterior lobes more rounded; but probably this only shows how prv 2

unreliable for diagnosis are slight or even moderately large differences in the shape of the ganglion in preserved specimens.

Contrary to Michaelsen, I found no copulatory glands in the segments behind the clitellum.

Each testis is divided into two lobes, one extending backwards ventrally, the other disposed vertically by the side of the alimentary canal, but the junction of the two is very broad and the lobes show little independence, unlike the numerous club-shaped lobes of the testes in the genus *Lumbricillus*, which are united only at the origin of their very attenuated stalks. The lower lobe may again show an incipient division. The male funnels are about three times as long as broad.

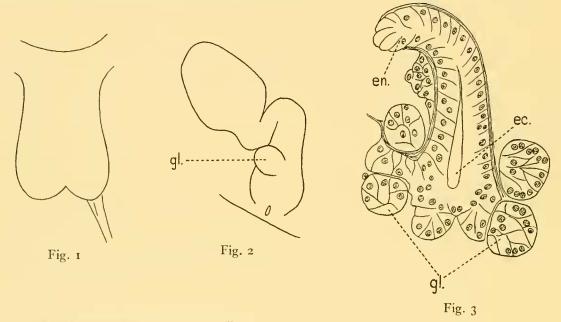


Fig. 1. Marionina georgiana; cerebral ganglion.

Fig. 2. Marionina georgiana; spermatheca, drawn from a whole mount; the full number of gland masses attached to the duct were not visible, only one (gl.) being well seen.

Fig. 3. Marionina georgiana; section through duct of spermatheca. A portion of the duct is cut lengthwise, the broader, ectal part of the duct (ec.) being below, the narrower, ental bent portion above (en.). A number (seven) of aggregates of gland cells (gl.) cluster round the ectal portion; the cells in these stain considerably less heavily than those of the duct itself. \times 500.

The spermathecae (Figs. 2, 3) have an ovoid or somewhat irregularly pyramidal ampulla, in length 100μ , prolonged at the ental end into a canal leading by a patent passage into the oesophagus. The tubular duct is well marked off, bent in the form of the letter S, and allowing for the bends is not far from twice as long as the ampulla; its diameter, at first $33-40\mu$, widens as it passes down, and the ectal portion of the duct is bulbous, 56μ in diameter. The epithelial cells which line the lumen of the duct become elongated and clearer in the bulbous portion, but are mostly still enclosed by the muscular coat. A few cell aggregates burst through the muscular coat, and form rounded lobes, of which one is seen in Fig. 2, and a number cut in section in Fig. 3. These

glandular lobes, not covered on the outside by the muscular coat, are (in the sexually mature specimen) 3 or 4 in number on one side and 7 on the other; the largest is 28 by 36μ as cut in section. (The gland masses were constantly two in number in Michaelsen's specimens.)

The species has been found in many various habitats, from purely marine (the canal system of sponges) and littoral (amongst roots of seaweeds and the rubbish of the shore), to purely fresh water (under stones in a pool) or more or less terrestrial (in moss).

Marionina grisea, sp.n. (Figs. 4, 5).

St. 189. 23. iii. 27. Port Lockroy, Wiencke Island, Palmer Archipelago. Shore coll. Three specimens, one small and non-sexual, one found on sectioning to be not fully mature, one sexually mature; along with *Lumbricillus maximus* and *L. lineatus*.

The longest specimen measures 14 mm., the next 11 mm.; diameter of the longest 0.68 mm. Segments 40, 33.

The worms are pigmented black on the dorsum; the pigment extends about as far as the level of the upper border of the ventral setal bundles, though it is thinner in the region between the lateral and ventral bundles. The pigment, while extremely dense dorsally in the most anterior segments, is very scanty, though, as seen in sections, not quite absent, in these segments ventrally. The youngest specimen is not so darkly pigmented, and in it the pigment extends downwards on each side only to the level of the lateral setae or very little below this. The pigment is situated below, not in, the epidermis; in the youngest specimen it forms a branching and anastomosing network, as if composed of branching chromatophores (though no nuclei are visible); in the largest specimen, as viewed whole, the black pigment is largely broken up into discrete roundish particles, though in some parts the chromatophore-like arrangement persists. In sections, the pigment appears as a brown granular deposit on the inner side of the body wall and in the muscular layer.

The prostomium is short, rounded, hemispherical. A head pore is apparently present.

The setae are lumbricilline in form; the ventral bundles comprise (6) 7 (8) setae in front of the clitellum, and the same number behind, falling at the hinder end to 4 or 5; the lateral bundles contain 4 or 5 in front and about the same number behind the clitellum.

The clitellum extends over segments xii-xiii; it is absent in the mid-ventral region. There is in the sexually mature (but not in the early sexual) specimen, ventrally in segment 10, a plate of thickened superficial epithelium, a single layer of tall cells, which contrasts strongly in its regularity, flatness, and equal thickness over its whole extent, with the thin (cubical or even lower) epithelium of the ventral surface of the segments behind it, and also with the more irregular epithelium of the segment. The epidermis of these anterior segments is only half as thick as that of the plate in x, 20μ as against 40μ ; while the thickness of the ventral epithelium of segments xi and xii is less again.

The gland cells in the integument, with their deeply staining contents, are arranged in transverse rows (as for example in *Lumbricillus lineatus*).

The body-cavity corpuscles are disc-like and subcircular, oval, somewhat triangular, or irregular in shape, with a spongy appearance when stained, and containing a small round homogeneous nucleus; in their greatest diameter they measure $25-35\mu$. Sometimes they appear to be degenerate, and coalesce into a loose network or an irregular coagulum-like mass.

Septal glands are present in segments iv, v and vi; from the posterior pair a large irregularly lobed mass projects on each side extensively into vii, reaching backwards more than half-way through the segment; these posterior lobes are covered by a fine membrane derived from septum 6/7, and represent as it were a hernia of the cell mass into the segment behind.

Salivary glands are absent. Postpharyngeal bulbs are, however, typically present, as usual in this genus and in *Lumbricillus*.

The chloragogen cells of the intestine show large vacuoles; a single vacuole may take up the greater part of the cell, or there may be more than one vacuole in a cell; the appearance is such as might result from large droplets of fatty matter having been dissolved out.

The dorsal vessel begins in segment xiii in one of the sectioned specimens, in xii in the other.

The preseptal part of the nephridia is small, and narrows slightly towards the septum ; it comprises, however, somewhat more of the organ than merely the funnel. The shape of the postseptal varies—short and rounded, or more elongated. The duct also varies ; in the postclitellar region it is short, and passes from the hinder and lower part of the organ downwards, or somewhat forwards or backwards, to the surface; it appears rather as if there were really no proper duct, the postseptal being bent at its hinder end, and narrowing, like an inverted cone, to reach the surface. In front of the clitellum, however, there really is a duct from the hinder end, at right angles to and as long as the postseptal.

The testes are already large even in the younger of the two sectioned specimens, and form each an elongated triangular mass, invested for the most part by a loose membrane, which is, however, lacking over a portion of the distal end of the gonad. This end is breaking up, and setting free masses of male cells; and large numbers of these developing sexual cells are free in the cavity of the segment. The body of the testis shows a tendency to cleave lengthwise, with the formation of a number of elongated clubshaped lobes not unlike those of *Lumbricillus*; the process is a cleavage only, not a separation, though in some sections a membrane can be seen between the lobes, like the membranes which envelope the club-shaped lobes of the testes of *Lumbricillus*.

The funnels are relatively short, 3 to $3\frac{1}{2}$ times as long as broad; the lip at the open end of the funnel is quite narrow and scarcely everted. The vas deferens, confined to segment 12, forms a loose coil, which pierces through a rudimentary penial body to end on a small rather indefinite male papilla.

The penial body (Fig. 4) is in considerable part embedded in the body-wall. It consists of (a) a number of much elongated cells, vertical to the surface, forming a mass 100μ in antero-posterior extent and 65μ in height; this is pierced by (b) the end of the vas deferens, and (c) also by the stalks of two large glands, the "prostates"; these structures are covered in by (d) a layer of muscular fibres, really the longitudinal layer of the body-wall, which appears here as the fairly definite capsule of the cell mass; adding the thickness of this capsule to the height of the cells, the vertical extent of the penial body is 78μ . The prostates (Fig. 4) are two on each side, one anterior and one

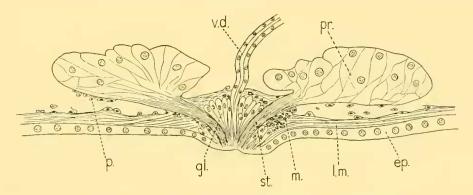


Fig. 4. *Marionina grisea*; prostates and "penial body" (combined from several sections); \times 220. *ep*. surface epithelium; *gl*. glandular cells of the rudimentary penial body; *l.m.* longitudinal muscular layer of body-wall (the circular layer is not visible here); *m.* muscular fibres filling up angle between stalk of prostate and surface layers, and covering in gland cells of penial body; *p.* peritoneal cells; *pr.* "prostate"; *st.* stalk of prostate; *v.d.* vas deferens.

posterior; each is a conspicuous, somewhat flattened mass (flattened from above downwards) of spongy-looking gland cells, 200μ in antero-posterior and 240μ in transverse

measurement; the glands thus take up a good part of the width of the segment. Each has a stalk composed of the aggregated thread-like prolongations of the cells; the stalks converge in the penial body, and eventually reach the surface close to the opening of the vas deferens.

The spermathecal apparatus (Fig. 5) consists of ampulla, duct, and glands, the duct being the largest portion of the whole. The ampulla is only slightly swollen (*ca.* 74 μ in diameter), in the main tubular, about 120 μ long; it is lined by cubical epithelium, and communicates by a narrow but patent passage with the oesophagus. The duct is bulbous or subspherical in shape, with a diameter of 110 μ and a height of about 120 μ ; its lumen is narrow, and lined by elongated cells with nuclei at their bases; a muscular coat envelopes the bulb, and the heads of spermatozoa pointing down-

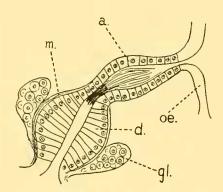


Fig. 5. Marionina grisea; spermatheca, in section, diagrammatic. a. ampulla; d. the bulbous duct; gl. gland mass; m. muscular layer of duct; oe. oesophagus. Spermatozoa are seen in the lumen, their heads in the constriction between ampulla and duct, their tails pointing upwards.

wards occupy the upper part of the lumen. The change in character of the lining epithelium, tall in the bulb (duct), low in the ampulla, is quite sudden. There are two, or sometimes three, glands in connection with the duct, attached to its lower portion.

There is a copulatory gland in segment xv, of some size, consisting of two halves, one on each side of the cord; each half is bilobed, the lobes being anterior and posterior, and the cord is not in the least covered over, the dorsal surface being quite free; indeed the gland does not invest the cord closely even at the sides, the two halves being thus quite separate. The gland rises up to a height of 100μ above the inner surface of the bodywall—double the height of the upper surface of the cord—but still does not reach the level of the gut.

The relations of this species will be considered along with those of the next.

Marionina aestuum, sp.n.

11. i. 27. Shore of Bay of Isles, South Georgia; from Ulva sp. between tide marks. Several specimens, some sexual; along with *Enchytraeus colpites*.

The length of the sexual specimens is 11–12 mm., and their diameter 0.6 mm., or slightly more at the clitellum. Segments 46, 47, 48.

The prostomium is short and rounded.

This, like the last, is a pigmented species; the pigment varies in depth from light to dark grey, and extends from the dorsal surface downwards on each side as far as the level of the ventral setae, or more densely to the level of the lateral setae and thence more lightly to the ventral setae. On a casual examination it appears never to extend all round the body; but a careful inspection in cedar oil showed that in the most anterior segments a number of scattered chromatophores are present in the ventral region also. As seen in sections the brown branched chromatophores are quite below the epithelium, in the longitudinal muscular coat and especially in a layer on the inner surface of this coat.

The setae are lumbricilline in shape, and are rather uncommonly numerous in each bundle. The ventral bundles comprise 14–17 setae in front of the clitellum; behind, 8–15 are found, the higher number only occasionally, the lower usually towards the hinder end of the body. The lateral setae are 8–13 per bundle in front of the clitellum, and 7–9 behind.

The clitellum, occupying segments xii–xiii, is saddle-shaped, very thick dorsally, absent ventrally, and lighter in colour than the neighbouring segments; there is a ventral groove between the well-marked lower border of the clitellum on each side; and the male porophores, situated at this lower border, look almost inwards. The appearance varies somewhat, however, probably with the degree of contraction of numerous muscular bands internally in this region. There is no ventral thickened cutaneous plate in segment x, as in *M. grisea*.

The epidermis contains very numerous and closely set gland cells, staining so deeply blue (with haematoxylin) as to appear black; indeed for a moment on first looking at the sections I doubted if the colour of the worms might not be due to these cells. The depths of the intersegmental grooves, and the areas immediately surrounding the setal bundles,

are free from these glands. The chromatophores are at a deeper level, are brown in colour, and branched; the pigment is in the longitudinal muscular coat and especially in a layer on its inner surface (cf. *M. grisea*).

The body-cavity corpuscles are small; many are spindle-shaped, mostly *ca.* 20μ in length, though sometimes as much as 30μ ; others, about the same length, are much broader and subcircular in form; all are nucleated, the cell body staining lightly with eosin and granular in constitution.

The postpharyngeal bulbs are the best-developed examples of these enigmatical structures that I have ever met with. There are no salivary glands.

The septal glands are bulky, and take up a good deal of room in segments iv-vi; those of vi project back a long way into vii. In the second series of sections to be examined there was in segment vii a separate septal gland, not a part of that belonging to vi. Its connection with the gland in vi was effected by a non-staining stalk or strand (as the septal glands in each successive segment are always connected to those in front), and it passed backwards through a definite opening in septum 7/8 (not merely bulging this septum backwards) so as to occupy also the anterior part of segment viii. Altogether, therefore, the extent of the glands was quite unusual in this specimen.

The chloragogen cells of the anterior segments contain much brown pigmented matter.

The dorsal vessel arises in segment xiii, through the whole length of which it extends. From the staining reaction of its contents with eosin the blood presumably contained haemoglobin and was red in life.

The nephridia possess each a rather bulky anteseptal portion, with a cylindrical funnel and, in addition, an amount of glandular tissue; the anteseptal (82 or even perhaps 90μ) is nearly as long as the postseptal (100μ). The duct is as long as the postseptal; it may be given off from the lower surface of the postseptal some little distance from the hinder end of the organ, when it takes a curved course to the surface; its lumen is dilated, apparently forming a sort of reservoir, where it enters the body-wall. The place of origin of the duct, however, seems to vary; from the evidence of longitudinal sections it may be given off from the middle of the postseptal, or even from quite near the septum.

The testes are small organs, each consisting of 4 or 5 cylindrical or slightly clubshaped or pear-shaped lobes surrounded by no obvious capsule; the type of organ is really that characteristic of the genus *Lumbricillus*, since the organ is divided down to its base. Segment xi contains a large number of free male cells in various stages of development (morulae, bundles of spermatozoa)—so many that the anterior septum is much bulged forwards, nearly to the level of furrow 9/10; the ends of the testis lobes break up, and the cells become free, much earlier than in most species of *Lumbricillus*, so that the testes are here much smaller organs than usually in that genus.

The male funnel is about $2\frac{1}{2}$ times as long as broad; it is a stout organ, about half as broad as the available diameter of the segment; its everted rim or collar is narrow and projects only slightly. The vas deferens, 13μ in diameter, is a loose coil of no great length; it reaches the surface through a cleft in the muscular mass which represents the penial

body, then runs between the stalks of the two "prostates" (v. *infra*), and finally penetrates the junction of the two stalks and the mass of cells which mingles with them where they abut on the surface.

The "prostate" glands, in segment xii, are very large, and lie, one anterior and the other posterior in position, against the lateral body-wall; the hinder end of the anterior touches the front end of the posterior gland. Each is a solid mass, in length $240-320\mu$ by about 280μ in breadth, and is rather deeply lobed; the cells are prolonged into much elongated and fine thread-like stalks, along which the secretion probably passes, and which are aggregated to form a stalk for each gland; these stalks enter the body-wall, converge, and meet at the surface.

There is no definite penial body, that is, no definitely limited, spherical, encapsuled mass, composed mainly of elongated cells abutting on the terminal part of the vas deferens and the surface invagination into which the vas discharges. The stalks of the prostates, however, are enclosed in a loose mass of muscular fibres which run in many directions—a spongy mass, not of very definite outline, and not encapsuled but continuous with the tissues of the body-wall. This mass fills out the interior of the porophore, a projection of some size, at the tip of which is a special rounded aggregate, 100μ high, of moderately deeply staining cells derived from the surface epithelium; the stalks of the prostates, and also the vas deferens, enter and come to the surface through this aggregate, the elements of which the stalks are composed (the prolongations of the gland cells) mingling indistinguishably with the cells.

There is a much greater amount of muscular tissue in this "bulb" than in the corresponding structure of M. grisea; the mass has a vertical thickness of about 250μ , and envelopes the whole of the stalks of the prostates, comes into extensive contact with the base of the glands, and even surrounds their lower parts.

Many muscular strands pass inwards from the body-wall in the region of the male pores.

The spermathecal apparatus on each side (ampulla plus duct) forms a tube, the diameter of which does not vary very much from one part to another, the ampulla, however, being rather narrower than the duct (diameter of ampulla 70μ , of duct 85μ ; or ampulla 61μ , duct 74μ), and about equal to it in length (about 160μ). The ampulla communicates by a patent passage with the oesophagus; in one specimen a plug, composed of the tails of spermatozoa, occupies the tubular passage through the oesophageal wall. Though there is no very sharp external limitation between ampulla and duct, the character of the epithelium of these two parts is quite different; the high clear cells of the duct give place abruptly to the low, more deeply staining cells of the ampulla, so occasioning a sudden change in the width of the cavity of the organ. The lumen of the duct contains the heads of numerous spermatozoa.

Associated with the spermatheca of each side are two masses of gland cells, one above and one below the ectal part of the duct, each mass about as thick as the duct. The stalks of these gland masses enter the muscular layer of the body-wall, and probably reach the surface close to the spermathecal pore; they do not discharge into the spermathecal duct, which is everywhere enclosed by a muscular investment.

A copulatory gland, small and asymmetrical, is present in segment xiv, and another, still smaller, in xiii.

In 1905 Michaelsen described (1905 *a*) from Kerguelen Island (in the southern part of the Indian Ocean) a dorsally and laterally pigmented worm which he named *Marionina werthi*. The chief characters were: a maximum number of 10 setae per bundle; testes (apparently of small size) consisting of a small number of separate cord-like lobes (i.e. "divided"); funnels probably about five times as long as broad; penial body bulbous, small, embedded in the body-wall; a single prostate; spermathecae broadly spindle-shaped, no distinct duct, no glands; copulatory glands in xiv, extraordinarily large, extending upwards towards the dorsal surface.

In 1922 Benham (1922) discovered amongst the worms collected on Macquarie Island (to the south of New Zealand) similarly pigmented specimens, which he supposed to belong to Michaelsen's species, and which he therefore did not describe fully, contenting himself with giving the points in which they differed from the latter author's description. Thus they had a maximum of 13 setae per bundle; the prostates were "some in front of, and others behind the sperm pore" (they are shown in the figure as in two groups, an anterior and a posterior, opening independently of each other and of the vas deferens); no penial bulb; the spermathecal ampulla considerably wider than the duct, from which it is distinct; two gland masses opening into the ectal end of the duct.

M. grisea, from the Palmer Archipelago, described on p. 243, has much the same pigmentation as the two foregoing groups of specimens (apparently less pigment is present on the ventral surface of the anterior segments); the maximum number of setae per bundle is 8; the testes are large, and show a commencing cleavage into lobes like those of *Lumbricillus*; the funnels are $3-3\frac{1}{2}$ times as long as broad; the prostates are two on each side, anterior and posterior; the penial bulb is of small size, not distinctly encapsuled, somewhat indefinite in its limits, and mostly contained within the body-wall; the spermathecal duct is bulbous in form, broader than the ampulla, and has two glands associated with it; the copulatory glands are in xv, and do not reach the level of the intestine; there is a thickened ventral plate of epithelium in segment x.

Finally *M. aestuum*, from South Georgia, has the same pigmentation as the last; the maximum number of setae per bundle is 17; the testes are small, and consist of a small number of separate cord-like lobes ("divided"); the funnels are $2\frac{1}{2}$ times as long as broad; the prostates are much as in *M. grisea*; a penial bulb can scarcely be described, but a large spongy muscular mass envelops vas deferens, stalks of prostates, and a group of gland cells; the spermathecal apparatus is tubular, and the duct distinct, broader than the ampulla, associated with two gland masses; copulatory glands in xiii and xiv, small or very small; no ventral plate in x.

We may first compare Benham's worms with *M. werthi*. Benham implies that the structural differences between his specimens and Michaelsen's are sufficiently great to justify their separation as a distinct species—or at least would be so, were it not for the similarity of pigmentation ("were it not that the pigmentation is so unusual I should be inclined to make a new species for it"). Thus in *M. werthi* the spermathecal apparatus

is broadly spindle-shaped, and there is neither a distinct duct nor any associated glands; in Benham's worms the ampulla and duct are distinct, the ampulla being (from the figure) considerably wider, and there are two glands. Further, there is a small penial body in *M. werthi*, none in Benham's specimens; one prostate, apparently, in *M. werthi*, but a number of glandular masses aggregated into a few groups in Benham's worms. If the two worms described above (*M. grisea* and *M. aestuum*), with the same pigmentation, possess, like Benham's specimens, distinctive structural differences such as would ordinarily be sufficient to characterize separate species, then I think Benham's reason for merging his worms with Michaelsen's will disappear, and we shall have a group of species, closely related, no doubt, with the peculiar pigmentation as a common feature.

The worms which I have called M. grisea differ from M. werthi principally in the testes (massive, with clefts in their substance but not divided into free club-shaped lobes); in a very distinct division of the spermathecal apparatus into bulbous duct and spindle-shaped ampulla, and in the presence of two associated glands; in possessing two large and definite prostates; and in having copulatory glands, of only moderate size, in segment xv (instead of very large glands, in xiv).

The specimens from South Georgia, *M. aestuum*, are distinguished from *M. werthi* principally by the extraordinarily large number of setae per bundle; the tubular spermathecal apparatus with well-defined duct and associated glands; the prostates, as in *M. grisea*; the small or very small copulatory glands in xiii and xiv; and probably by considerable differences in the penial body. *M. aestuum* is distinguished from *M. grisea* by the number of setae per bundle, the form of the spermathecal apparatus, the small and divided testes, the copulatory glands in xiii and xiv (instead of in xv only), and by the absence of the ventral epithelial plate in x.

The value of this last feature is not quite certain; it is not described in M. werthi or by Benham for his specimens, but it might possibly have been overlooked, or not thought worthy of mention. It appears definitely to characterize M. grisea as contrasted with M. aestnum.

On the whole I consider that the differences between these four forms, especially in the spermathecal apparatus, and in a somewhat less degree in the testes, penial body and associated structures, and in the copulatory glands, are sufficient to justify their separation. They form a closely related group, but I cannot arrange them in a series showing, for example, a progressive evolution or regression of the distinctive characters according to distribution from west to east or *vice versa*. On the whole the group appears to be a primitive one; the testes show the first stages, but only the first stages, in the evolution of the condition characteristic of the genus *Lumbricillus*, and the lumbricilline penial body is either absent or present in a very indefinite form; the prostates, however, are a special development, not ordinarily found either in *Marionina* or *Lumbricillus*.

For the worms described by Benham (1922) I propose the name M. benhami.

The difference between the two genera *Marionina* and *Lumbricillus* lies in the testes massive in *Marionina* and not divided to the base, divided in *Lumbricillus* and forming numerous pear-shaped lobes attached by their narrow ends, each enclosed in a mem-

brane within which the sexual cells are shed and undergo their development into sperm morulae and spermatozoa. The four species here discussed are so closely related that they must obviously go in the same genus; but it is somewhat doubtful which this ought to be. It seems to me that the condition of the testes in *werthi* and *aestuum* resembles rather that of *Lumbricillus*, in *grisea* that of *Mariouina* (nothing is stated regarding the testes of *benhami*, which we may perhaps infer to resemble those of *werthi*). I place the whole group in the genus *Mariouina*, however, because Michaelsen (after some hesitation) decided to refer his species *werthi* to this genus.

Genus Lumbricillus, Örst.

Lumbricillus lineatus (Müll.).

Pachydrilus verrucosus, Ude, 1896, p. 3, pl., fig. 6 a, 6 b.

St. 122. 14. xii. 26. Maiviken, West Cumberland Bay, South Georgia. Shore coll. (salt water). A number of specimens; along with *Lumbricillus maximus*.

St. 166. 19. ii. 27. South-east point of Paul Harbour, Signy Island, South Orkneys. Shore coll. A number of specimens; along with *Lumbricillus maximus*.

St. 189. 23. iii. 27. Port Lockroy, Wiencke Island, Palmer Archipelago. Shore coll. Several specimens; along with Lumbricillus maximus and Marionina grisea.

The species is the same as that previously recorded, under the name of *Pachydrilus verrucosus*, by Ude from Tierra del Fuego (Ude, 1896). It is one of the commonest of the shore Enchytraeids of British coasts, and is well known from other European countries also, and from inland stations as well as from the coasts. It is a variable species, and has consequently been described under many names (cf. Stephenson, 1922).

In the specimens from Wiencke Island and from the South Orkneys the septal glands are remarkably small. As is commonly recognized, these glands often or usually consist in each segment (iv, v and vi) of a portion in close association with the posterior septum of the segment and often appearing to be contained between the two lamellae of the septum, and a forwardly projecting lobe on each side ventrally in the segment. In the specimens just mentioned the septal portions of the glands are reduced to a few cells only, between the two layers of the septa; the forwardly projecting lobes are also reduced, but not quite to the same extent. In the examples from South Georgia, however, the glands are of large size.

One of the most variable organs of this worm appears to be the male funnel; in the several descriptions of the species under its various names different proportions are given for the funnel, from 2 to 9 times as long as broad. In worms from one locality in Scotland I found the funnels from $2\frac{1}{2}$ to 6 times as long as broad (Stephenson, 1922), while in those from another place the funnels in the intact worm might be as much as 9 times, but might contract, on teasing the worms to isolate the internal organs, to as little as twice as long as broad (Stephenson, 1911 (*L. subterraneus*)). In the present specimens they appear to be in some cases 5 or 6 times, in others 8–10 times as long as broad.

A notable characteristic of the species is the presence of transverse rows of very deeply staining (with haematoxylin) gland cells in the integument.

3-2

Lumbricillus maximus (Michaelsen) (Fig. 6).

Pachydrilus maximus, Michaelsen, 1888, p. 56, pl. i, fig. 1 a-e. Lumbricillus maximus, Michaelsen, 1905 a, p. 10. Lumbricillus maximus, var. Robinson, Michaelsen, 1905 a, p. 11, pl. i, fig. 1.

St. 122. 14. xii. 26. Maiviken, West Cumberland Bay, South Georgia. Shore coll. (salt water). A number of specimens; along with *L. lineatus*.

St. 166. 19. ii. 27. South-east point of Paul Harbour, Signy Island, South Orkneys. Shore coll. A number of specimens; along with *L. lineatus*.

St. 179. 10. iii. 27. Melchior Island, Schollaert Channel, Palmer Archipelago. In creek to south of south-west anchorage. Shore coll. Numerous specimens.

St. 189. 23. iii. 27. Port Lockroy, Wiencke Island, Palmer Archipelago. Shore coll. A number of specimens; along with *Lumbricillus lineatus* and *Marionina grisea*.

St. MS 70. 9. iii. 26. Maiviken, West Cumberland Bay, South Georgia. Shore coll. A number of specimens.

The present species was first described by Michaelsen, from South Georgia, in 1888; in 1905 the same author gave additional particulars of its anatomy derived from specimens from other southerly latitudes (the Crozets and Kerguelen), and described a variety from New Amsterdam Island (in the south of the Indian Ocean). The following notes, however, are perhaps not quite superfluous.

The longest specimen met with measured 45 mm.—a giant among Enchytraeids; others were 40 mm., others 30 mm. and less; mature worms were found of all sizes down to 17 mm., and some even shorter—13, 12, and 11 mm. The number of segments did not vary as much as the length, the limits, among the worms whose segments were counted, being 55–70, and commonly the number was not very far from 60.

The ventral setae are (3, 4) 5, 6, 7 per bundle in front of the clitellum, and (3) 4, 5 (6) behind; the lateral (3) 4, 5 in front of and (2) 3, 4 behind the clitellum.

In the integument are numerous gland cells staining very deeply with haematoxylin, arranged in transverse rows, as in *L. lineatus*.

The septal gland of segment vi bulges backwards into vii; the portion which is in relation to septum 6/7 pushes back the septum (or the posterior of the two lamellae of the septum; cf. what was said under *L. lineatus*) after the manner of a hernia, and may thus reach the level of septum 7/8.

There is a pair of postpharyngeal bulbs, in the usual situation.

The dorsal vessel usually begins, as described by Michaelsen, in xv, but occasionally further back, in xvi or xvii. The blood stains (haematoxylin and eosin) a dull dark purple, which probably indicates that it contained a little haemoglobin during life.

The male funnels vary much in length, from as little as 3-5 times as long as broad to as much as 7-9 times, or even 10 and possibly 12 times; but Michaelsen's figure of about 8 times is a fair average estimate. They sometimes (? always) become narrower backwards; thus in one case the diameter at the anterior end was 160μ , at the hinder end 110μ ; the hinder end may project back in a cone-like manner through septum 11/12. The rim or flange at the anterior end is (? always) enormously broad, as shown in Fig. 6.

The penial body constitutes a subspherical mass about 200μ by 250μ ; it is surrounded by a strong muscular capsule, and contains much elongated gland cells as well as a stroma or scaffolding of muscular or connective tissue strands.

The spermathecae of these specimens agree with Michaelsen's corrected description (Michaelsen, 1905 a). I made a very considerable number of series of sections from the

five batches of specimens of this worm, and in describing them my notes more than once say that the duct is marked off from the ampulla; but from drawings made at the same time this marking off appears to be due, as in Michaelsen's specimens, to a kinking at this place. In other examples the short, somewhat bent duct soon widens, its high columnar epithelium becomes gradually lower, and without distinct demarcation the duct becomes the ampulla. The ectal end of the duct is surrounded by a crown of gland cells, relatively smaller than in L. lineatus, and slightly lobed; the cells composing this mass are, as usual, epithelial cells of the duct lining, greatly elongated, extending outwards far beyond the muscular investment of the duct.

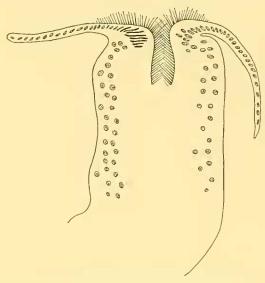


Fig. 6. Lumbricillus maximus; male funnel as cut in one of the sections, showing the relatively very broad rim. \times 210.

The copulatory glands are, as in Michaelsen's specimens, in segments xiv, xv and xvi.

I have previously (p. 237) described the degenerative changes which are very frequently found affecting the internal organs in this species.

Michaelsen (1905 *a*) described from New Amsterdam Island a var. *Robinson* of this species, characterized by its smaller size (12-16 mm.) and by the penial body being divided into two lobes by a transverse cleft, as well as, apparently, by the shorter nephridial duct. In my specimens the length is graduated from 45 mm. down to 11 mm.; I did not notice among the shorter specimens the other distinctive features mentioned by Michaelsen, but I cannot affirm their absence.

Some time ago I suggested (1922), without having any direct acquaintance with *L. maximus*, that it might be identical with *L. lineatus*. Now, after having at my disposal a large number of examples, I do not think it is, though it is very closely related. The arrangement of the gland cells in the superficial epithelium in regular transverse rows is suggestive of identity, and also the wide variability in the proportions of the male funnel in different specimens. Indeed, bearing in mind the variability of *L. lineatus*, the only distinction I can point to is in the spermathecae, and even here the difference is by no means so clear-cut as one could desire; in neither species is the duct sharply marked off from the ampulla; but the form of the ampulla is spindle-shaped in *lineatus*, more swollen, on the whole, and more irregular, and the duct relatively narrower, in

maximus; while the glands round the ectal end extend much further up the duct—as far as the base of the ampulla—in *lineatus*.

Lumbricillus macquariensis, Benham (Fig. 7).

Lumbricillus macquariensis, Benham, 1905, p. 295, pl. xiv, figs. 8, 11, 12, 13. Lumbricillus intermedius, Benham, 1909, p. 261, pl. x, figs. 8–11. Lumbricillus macquariensis, Benham, 1915, p. 189. Lumbricillus macquariensis, Benham, 1922, p. 6. Pachydrilus intermedius, Michaelsen, 1923, p. 197.

Undine, South Georgia. iii. 26. Six specimens, mostly mature. Note by collector: "Specimens of Crustacea, Oligochaeta, Coleoptera, dipterous larvae and puparia, and apterous Diptera found living together under stones on the upper edge of the beach at Undine Harbour, South Georgia."

The present species has hitherto only been known from the islands to the south of New Zealand (Macquarie, Auckland and Campbell Islands); it is interesting, therefore, to find it now in South Georgia in the same latitude as these islands but distant from them by nearly half the circumference of the globe. Since this distribution is possibly of some importance, I give below some particulars which will permit other workers to check my identification.

The specimens are the stoutest worms in the present collection; the largest is about 22 mm. long (all are more or less curled) and 1.25 mm. thick, while a smaller one, also sexually mature, is 15 mm. long and 1 mm. thick. The largest has 72 segments, the smaller specimen 52; the external segmentation is well marked. I did not find the prostomium as in Benham's *L. intermedius*—"rather long, about equal to the first two segments together"—but blunt and rounded.

The ventral setae are 6(7) in the preclitellar, (4) 5, 6 in the postclitellar bundles; the numbers for the lateral setae are 5, 6 and 4, 5 respectively.

The clitellum, as seen in sections, includes segments xii and xiii and encroaches slightly on xi and xiv; it is absent mid-ventrally.

There are numerous deeply staining gland cells in the integument, in irregular transverse rows; the furrows, however, are free from these cells.

The coelomic corpuscles are subcircular or irregularly shaped disks, $18-24\mu$ in diameter, nucleated and of granular constitution, numerous and all of one kind.

The septal glands are bulky; the hindmost, belonging to segment vi, projects backwards into vii so as to reach a level not far from septum 7/8.

Postpharyngeal bulbs are present, as usual in the genus, but no salivary glands.

The dorsal vessel begins in segment xv; the intestinal sinus may be somewhat swollen dorsally in xvi, though a definite vessel does not seem to be present here.

The nephridia are conspicuous organs in sections, more so than usually. The anteseptal is small, though it includes a little more of the organ than merely the funnel. The postseptal seems contracted antero-posteriorly, short and "hunched up" in appearance, and may be of greater extent vertically than from front to back. The duct is given off from the hinder end of the organ, and is usually longer than the postseptal—indeed it may be quite double the length; it passes down, or sometimes downwards and back-

wards, or with an S-shaped curve, to the surface; its ectal portion is wider, and except, apparently, when the duct is put on the stretch has a distinct cavity or small reservoir.

The male funnels are about 5 times as long as broad, and possess a broad flange-like rim.

The spermathecal ampulla (Fig. 7) is of a somewhat oblong shape, and about $1\frac{2}{3}$ times as long as wide; it communicates with the oesophagus by a narrow passage which runs out to a point at the oesophageal wall; the opening is scarcely patent in these specimens.

The duct is about half as long as the ampulla, and less than half as wide, and the separation between duct and ampulla appears at first to be fairly definite. In a longitudinal section of the organ, however, the tall columnar cells of the duct extend far into the ampulla—to nearly half its height, where they suddenly give place to a much lower, approximately cubical epithelium, which lines the upper portion of the cavity. Around the base of the duct, not covering its whole length, is a crown of gland cells, a lobed mass consisting really of some of the cells of the lining epithelium of the duct which have elongated outwards through the muscular layer of the duct. Not all the epithelial cells of the ectal end of the duct are thus elongated; there is still an epithelial lining with nuclei basally situated, then on the outside of this layer a thin muscular coat with interruptions for the passage of the elongated gland cells, and then the bodies of these cells with their nuclei irregularly distributed.

Copulatory glands are present in five segments, xiv-xviii; in the anterior segments of the series they are of moderate size—largest, and equally large in xiv and xv; they then diminish in size backwards, and in xviii are very small. All leave the dorsal surface of the cord free. My series of sections do not go back beyond xviii, but from the small size of the glands in this segment it seems improbable that there should be any more behind this point.

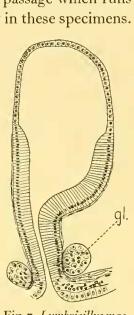


Fig. 7. Lumbricillus macquariensis; spermatheca in section, showing sudden transition of cubical epithelium of upper part of ampulla to high columnar of lower part of ampulla and duct. gl. gland mass forming a crown round ectal end of duct.

The correspondence between these specimens of mine and Benham's worms is close. The number of copulatory glands is larger than that given by Benham, though as an exception the present number (five) was even exceeded by one of Benham's specimens. Similarly, though in his worms the dorsal vessel did not usually arise in xv, it did so occasionally. Septal glands are said by Benham to be present in vii; possibly the condition is really not unlike that described above.

Most of the other features are sufficiently similar in Benham's worms and mine to call for no remark.

Lumbricillus antarcticus, sp.n. (Fig. 8).

St. WS 62. 19. i. 27. Wilson Harbour, South Georgia. From haul labelled "Moss dwellers" (the above is taken from the label; in the Station List WS 62 consists of two hauls, from 15-45 and 26-83 m. respectively). Five specimens; along with a specimen of *Hesperodrilus* sp.

Length 6-7 mm.; diameter 0.43-0.52 mm. Segments 35-38.

Prostomium rounded, hemispherical. Head-pore between prostomium and segment i. Setae lumbricilline in shape; the numbers vary within rather wide limits—in the ventral bundles 3–7 per bundle in front of the clitellum, 3–6 per bundle behind; the corresponding figures for the lateral bundles are (2) 3–5 and 2–5 respectively.

The clitellum embraces segments xii-xiii; it is absent ventrally and is not well marked even dorsally.

There are no rows of deeply staining gland cells in the integument.

The body-cavity corpuscles are oval or of an elongated pear shape, $18-20\mu$ in longest measurement; they stain very deeply, the nuclei appearing as a clearer area in the centre.

The septal glands are fairly bulky, but those belonging to segment vi do not push back in any marked degree into vii (as, for example, in *L. maximus* and *L. macquariensis*).

A pair of postpharyngeal bulbs are present, as is the rule in the genus; these appear to take the place of salivary glands which, as usual, are absent.

There is no sudden widening of the oesophagus to become the intestine; there is a slight localized dilatation in segment x, and another in xiv, but it seems doubtful whether these have any importance.

The dorsal vessel originates in segment xiii.

The anteseptal portion of the nephridium is small, but nevertheless comprises a little more of the organ than the mere funnel. The duct is given off from the hinder end; it is half as long as the postseptal or sometimes more—almost as long as the postseptal, and passes downwards and somewhat forwards.

The testes consist of large, typically pear-shaped lobes, containing within the investing membrane male cells, morulae in various stages of development, and ripe spermatozoa. The lobes radiate from their attachment at their narrow ends in a fan-like manner (as seen in longitudinal sections), forwards into segment x and backwards into xi; one large lobe gets into ix and one into xii (in the specimens sectioned).

The funnels are remarkably short, only $1\frac{1}{4}$ or $1\frac{1}{5}$ times as long as broad at their free end; in shape they are rather triangular or pear-shaped, becoming very much narrower at their base where they pass into the vas deferens; there is no projecting flange-like rim. The vas deferens is confined to segment xii, forming a close coil behind septum 11/12; it is relatively stout, 16μ in diameter. The penial body is of the usual lumbricilline type, roundly ovoid in shape, with a muscular capsule, the longer (antero-posterior) diameter $200-240\mu$.

The spermathecal ampulla (Fig. 8) is somewhat spindle-shaped or rather perhaps of an inverted pear shape; its ental end is prolonged to the oesophagus, with which it communicates by a patent passage; spermatozoa are seen to be attached to and to

penetrate within the epithelial layer of the ampulla. The duct is short; the narrow lumen of the duct expands rather suddenly at its upper end to become the cavity of the ampulla; in this sense ampulla and duct are fairly well marked off from each

other, though externally there is no very precise delimitation. A complete circle of glands surrounds the whole length of the duct and embraces the base of the ampulla; the glandular mass is lobed, and consists of the bodies of the cells of the duct epithelium, all the cells being prolonged through the muscular coat, which is visible as a single layer of fibres running longitudinally on the duct; there are no nuclei in the basal portions of the cells internal to the muscular layer.

Copulatory glands are present in segments xiii, xiv and xv; they are of moderate size, and leave the dorsal surface of the cord quite free; those in xiii are rather smaller than those of the other segments.

The present species is related not distantly to *L. lineatus*, but appears to be distinguished from it by the shortness of the male

funnel; it is alone among the southern species of this genus in having these proportions.

Genus Enchytraeus, Henle

Enchytraeus albidus, Henle.

Enchytraeus humicultor, Ude, 1896, p. 26. Enchytraeus humicultor var. similis, Ude, 1896, p. 27. Enchytraeus albidus, Michaelsen, 1903, p. 142. Enchytraeus albidus, Michaelsen, 1905, p. 8. Enchytraeus albidus, Michaelsen, 1905 a, p. 17. Enchytraeus albidus, Benham, 1905, p. 295.

St. 122. 14. xii. 26. Maiviken, West Cumberland Bay, South Georgia. Shore coll., fresh water. Several specimens, mostly with signs of sexual maturity.

Same locality and date. Under stones near upper lake; along with *E. australis*. Several specimens.

This is one of the Enchytraeids of the northern hemisphere which is also found in southerly latitudes; in the list of papers given above it is recorded from South Georgia (Bay of Isles), Tierra del Fuego and the Straits of Magellan, the Falkland Islands, the Campbell and Macquarie Islands, Kerguelen, and the Crozets. With the possible exception of *Lumbricillus lineatus*, it is perhaps the commonest member of the family in Europe; *L. lineatus* is found predominantly on the shore, but also inland, while *E. albidus* is predominantly terrestrial but is also found on the shore.

The sections of the present specimens attracted my attention by reason of the very wide central lumen of the sperm funnels.

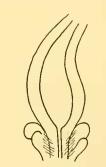


Fig. 8. Lumbricillus antarcticus; spermatheca as reconstructed from sections; a glandular mass envelopes the whole of the duct.

Enchytraeus australis, sp.n. (Figs. 9-11).

St. 122. 14. xii. 26. Maiviken, West Cumberland Bay, South Georgia. Under stones near upper lake. Several specimens; along with *E. albidus*.

St. WS 123. 8. vi. 27. Gough Island. Shore coll.; under bark of a rotten tree. Fourteen specimens.

Length 6–7 mm.; diameter o.3 mm. Segments 37–42.

Prostomium blunt, rounded. Head-pore between prostomium and segment i.

Setae enchytraeine in shape, the points fairly sharp; the setae are large and strong near the hinder end (length near the hinder end 76μ , in the anterior segments 64μ). The number per bundle is very fairly constant—three throughout the body, in both ventral and lateral bundles; two in the lateral bundles in segment xii and occasionally at the hinder end.

The clitellum, embracing segments xii–xiii, is not conspicuous, and is absent ventrally. The gland cells of the clitellum are arranged in regular transverse rows.

There are in general no deeply staining gland cells in the epidermis.

The coelomic corpuscles vary in their numbers; they are oval, pear-shaped, or spindle-shaped, 25μ in maximum length, rather darkly staining, with nuclei.

Salivary glands are present, arising from the recess behind the dorsal plate of the pharynx; they are twisted tubes, narrow but of varying diameter, and form a coiled mass which extends back into segment iv; I saw no branching.

There is no sudden widening of the oesophagus to form the intestine. In general, there is nothing remarkable about the chloragogen cells; they contain numbers of minute refractile particles, possibly oil-like globules (though any oily matter would have been dissolved out by the xylol in the preparation of the sections), appearing as scarcely more than dots even with the high power, in diameter about $I \mu$. Sometimes, however, in some parts of the body, the chloragogen cells are hollow, and appear as a small layer of protoplasm surrounding a central cavity—perhaps a space from which a fatty inclusion has been dissolved out.

The dorsal vessel begins in segment xiii.

The anteseptal portion of the nephridium is small, about twice as long as it is broad, and consists of the funnel only. The duct is about as long as the postseptal, and is given off often from the hinder end but sometimes from a place somewhat in front of this, running (observed chiefly in the posterior part of the body) downwards or downwards and forwards to the surface.

The cerebral ganglion is longer than broad (about $1\frac{1}{3}-1\frac{1}{2}$ times as long); its appearance, in two specimens, is shown in Fig. 9. The sides converge slightly forwards or are almost parallel; the hinder border is not sharply notched, but gently hollowed.

The testes are massive organs, each of which extends into the two segments x and xi, with one large lobe in each segment, the lobes being widely continuous ventrally between the segments; or the organ may be a single mass with hardly any distinction of lobes. Each testis is contained within a thin membrane, the testis sac, which encloses also male cells in all stages of development up to the ripe spermatozoa.

The male funnels (Fig. 10) are relatively small, and each appears to be triangular in shape; this is due to the organ being bent together on itself, as shown in the figure. This condition was seen in five sectioned specimens and in others examined whole, and appears therefore to be constant. As seen thus, the funnels are about as broad as long, but if straightened out they would probably be about three times as long as broad.

The vas deferens forms a coil, not large, but close, behind septum 11/12 and in front of the male aperture, in the anterior and ventral part of segment xii; it is 10μ in diameter, and enters the penial body on the dorsal side of the latter.

The penial body is of lumbricilline type—a definite, compact organ with muscular and peritoneal investments, regularly ovoid in shape except that it is indented—slightly bifid or bilobed—on its internal aspect; its antero-posterior length is 105μ and its height 70μ . There are no other glandular masses in relation with the male aperture.

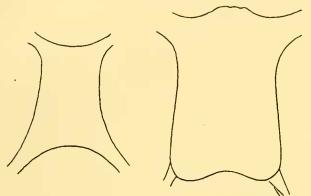


Fig. 9. *Enchytraeus australis*; cerebral ganglion; both forms were observed.

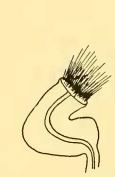




Fig. 10. Enchytraeus australis; male funnel.

Fig. 11. Enchytraeus australis; spermatheca.

4-2

As seen in specimens mounted whole, the spermathecal ampulla (Fig. 11) is of relatively small size, irregular in form, with a bulging on one side; in sections most of the series show it to be somewhat compressed antero-posteriorly; spermatozoa are seen pushing their heads into the epithelial lining; and there is a patent communication with the oesophagus. The duct is cylindrical, of some length—longer than the ampulla, but rather narrow (26μ) where not covered by glands; it is well marked off from the ampulla. The ectal half or rather more of the duct is covered all round by a glandular lobed mass, which as usual consists of the cells which line the lumen of the duct elongated and pushing outwards through the fibres of the muscular coat.

There are no copulatory glands.

For some time I thought it possible that the present specimens might be referable to Vejdovsky's *Enchytraeus buchholzi*, a common European species which has also been recorded from the Straits of Magellan (Ude, 1896). I have, however, decided to separate them as a new species on the following grounds:

(i) The number of segments—round about 40 in a considerable number of examples, as against 25–28 in *E. buchholzi*.

(ii) The almost absolute constancy of the number 3 for the setae in all bundles which (though given by Ude, for example, as the usual number) seems not ordinarily to be so definitely fixed in *E. buchholzi*; Michaelsen (in examples of this species which may constitute a distinct variety) found 3 in the preclitellar ventral bundles only, and elsewhere always 2; Vejdovsky's original account (1879) gives 2, 3 or 4 per bundle, Southern (1906) usually 3, often 2, rarely 4.

(iii) The shape of the funnel in the worms here described appears to be quite characteristic; I cannot recall that it has been described in any other Enchytraeid.

(iv) One of the chief features of *E. buchholzi*, mentioned in all descriptions, is the constitution of the large chloragogen cells, which are filled with large refractile oily globules. In sections, of course, the oil drops would have been dissolved by the xylol used in preparation, and would be represented by vacuoles; such vacuoles I have never seen in any of the several series of sections which I prepared, nor were any oil globules visible in the cells in whole mounts in cedar oil, nor in teased specimens. On the other hand, I have seen such vacuoles, answering exactly to Vejdovsky's description and figure (Vejdovsky, 1879) of those of *E. buchholzi*, in *E. colpites* (*v. post*), a species which, however, cannot be confused with *E. buchholzi*.

As less important points may be mentioned: (v) the fact that in E. australis the dorsal vessel originates within the clitellar segments, in E. buchholzi behind them; (vi) that the extent of the glands round the spermathecal duct is greater in the present specimens than in E. buchholzi; and (vii) that the salivary glands appear to differ considerably from those of E. buchholzi as illustrated and described by Vejdovsky, though it is possibly allowable to suspect some degree of schematization in this author's figure.

Enchytraeus colpites, sp.n. (Figs. 12, 13).

11. i. 27. Shore of Bay of Isles, South Georgia; from Ulva sp., between tide marks. Several specimens; along with Marionina aestuum.

Length 15-16 mm.; diameter 0.8 mm., or 1 mm. at the clitellum. Segments 37, 38, 39. Prostomium blunt, rounded.

Setae lumbricilline in form (with double curve); some, however, almost or quite straight at the distal end (enchytraeine). The ventral bundles contain (4) 5, 6 setae both in front of and behind the clitellum, the lateral (2, 3, 4) 5 (6) in front and (4) 5 (6, 7) behind.

The clitellum includes segments xii-xiii, and is absent ventrally.

There are no rows of large gland cells with deeply staining contents in the epidermis, but in each segment are to be seen two bands of small, scattered, deeply staining cells, one in front of and one behind the setal zone.

The coelomic corpuscles are spindle-shaped or oval, $25-36\mu$ in long measurement; they have not all the same appearance, some being granular and others more homogeneous in constitution.

The septal glands are large, and that of segment vi (in relation to septum 6/7) bulges backwards extensively into segment vii, so as to reach the hinder end of the segment.

There are no salivary glands, but a pair of postpharyngeal bulbs arise, as in the genera *Marionina* and *Lumbricillus*, from the recess behind the dorsal pharyngeal plate.

There is no sudden widening of the oesophagus. In specimens mounted whole the very dark chloragogen investment, beginning in segment v, is remarkable, and is rather characteristic of the species. The chloragogen cells are large and elongated, up to 57μ in height; the nucleus is not far from the middle, and the greater part of the interior of the cell is taken up by half a dozen or more large vacuoles, in series or sometimes two abreast (this appears to be the condition which is described for *E. buchholzi*). The very small (1 μ or less) brown chloragogen particles are numerous in the anterior segments.

The dorsal vessel begins at the anterior end of segment xiv, just behind septum 13/14 (in two sectioned specimens), or (in a third) extends through the whole of segment xiv. The blood stains red with eosin (indicating the presence of haemoglobin), and was therefore red during life; in some of the vessels are red-staining crystals, perhaps crystals of haemoglobin.

The nephridia present an extremely elongated funnel constituting the preseptal portion, 80μ in length by 20μ in diameter, with long cilia pointing down the tube and others directed outwards from the lip of the funnel. The shape of the funnel appears cylindrical in some cases, more conical, narrowed towards the septum, in others; this depends probably on the plane in which the part is cut; there are two, if not three, nuclei in the funnel, one being in the projecting part of the lip. The postseptal portion is about 150μ long; its apparent width depends on the plane in which it is cut—from 65 to 90μ . The duct, given off from the hinder end of the organ, leads downwards or downwards and forwards.

The cerebral ganglion (Fig. 12) is as broad as it is long, indented in front and behind, the sides converging forwards; the breadth at the widest part exceeds that at the anterior end in the ratio 40:27.

The proper testes are quite small, situated anteriorly and ventrally in segment xi, and cut up into a number of irregular, small, ovoid or shortly cylindrical lobes, which in many cases are seen to be surrounded by a delicate membrane. The testes consist only of sexual cells which have not begun to divide to form morulae; they differ altogether from the lobed ("divided") testes of the genus *Lumbricillus*, where the numerous large clubshaped lobes, each surrounded by a membrane, consist of undifferentiated sexual cells along with all stages—morulae, spermatids and spermatozoa—of their subsequent development. In the present species male cells in all stages of development

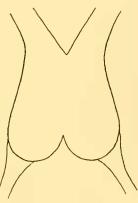


Fig. 12. Enchytraeus colpites; cerebral ganglion.

are found free in the cavity of segment xi, in such quantities as to bulge septum 10/11 forwards or 11/12 backwards. What happens therefore is that the enclosing membrane disappears at an early stage, and the lobes of the testis shed their cells into the body-cavity, where their ripening takes place.

The male funnels are of moderately large size, about 5 or 6 times as long as broad,

with a small everted rim at the mouth. In one specimen a rudimentary third funnel was seen, as a small bud on the side of one of the larger ones. I do not remember noticing this particular abnormality before. The vas deferens, 20μ in diameter, forms a close coil on each side, which may extend into the hinder half of the segment amongst the large ova.

The penial body is of the enchytraeine rather than of the lumbricilline type. It consists of a number of pear-shaped masses of gland cells, about eight such masses being visible in a single longitudinal section, and the total number on each side being perhaps in the neighbourhood of two dozen. These gland masses are closely compacted together, separated, however, from each other by, and each individual pear-shaped mass more or less enveloped in, muscular strands; there is no common capsule binding the whole together, and the upper (dorsal) ends of the masses are without covering. The glands are composed of cells derived from the surface epithelium, and discharge on the surface around the small aperture of the vas deferens, which comes to the surface after passing between the glandular masses. The muscular fibres which intervene between the gland masses belong to a numerous series of oblique strands which pass upwards from the neighbourhood of the male pore to the body-wall in the more dorsal part of the segment; a number of such strands occur also in segment xiii.

The spermathecal ampulla (Fig. 13) is elongated, pear-shaped, and passes without any sharp demarcation into the duct; it communicates with the oesophagus by a passage,

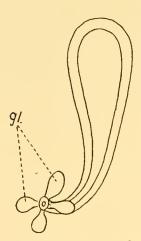


Fig. 13. Enchytraeus colpites; spermatheca. gl. glands at ectal end.

which can sometimes be seen to be patent, and is no doubt always so at some time of the sexual history of the animal; from some of the sections it appears as if the connection with the oesophagus were effected by means of a special diverticulum of the ampulla. The portion of the apparatus which serves as duct is curved; it has around its ectal end a number of small pear-shaped glands. These glands are derived from the surface epithelium in the immediate neighbourhood of the aperture, where they discharge, and are not, as is usually the case, cells of the lining epithelium of the duct which have elongated and burst through the muscular coat of the duct wall; they are three or four in number on each side—perhaps sometimes even fewer.

Copulatory glands are present and of moderately large size in segment xiv, spreading out to a distance of about 80μ on each side of the cord, but they do not cover its dorsal surface. In xiii are

smaller glands, as also in xi and x; these last (in x) are very small.

The present species occupies (like quite a number of other forms) a position between the genera *Euchytraeus* and *Lumbricillus*. Allying it with *Lumbricillus* are the lumbricilline setae, the red blood, and the postpharyngeal bulbs which replace the salivary glands; copulatory glands are also general in *Lumbricillus*, exceptional in *Euchytraeus*. But the most distinctive characters of the genus *Lumbricillus*—the numerous and large pear-shaped testicular lobes or sacs, each enclosing within a membrane all stages in the

development of the male cells, and the compact, ovoid, and encapsuled penial body with characteristic structure are absent, and are represented by the less specialized conditions found in *Enchytraeus*.

The specific name is taken from the Greek $\kappa o \lambda \pi i \tau \eta s$, dwelling on a bay ($\kappa o \lambda \pi o s$).

Genus Michaelsena, Ude

Michaelsena monochaeta (Michaelsen) (Fig. 14).

Enchytraeus monochaetus, Michaelsen, 1888, p. 66, fig. 6 a-c.

St. 159. 21. i. 27. 53° 52' 30" S, 36° 08' 00" W; depth of net 160 m. Net DLH (large dredge, heavy pattern). About a dozen small worms or fragments of worms, mostly bent or twisted.

The species was described by Michaelsen as long ago as 1888 from specimens taken in South Georgia. Identification is easy, by means of the setae. These conform entirely

to Michaelsen's description—a single seta only per bundle, the ventral setae beginning in segment v, the lateral in xvii or thereabouts; I find a slight distal curve in some (lumbricilline setae). The spermathecae (Fig. 14) show a broadly pear-shaped ampulla with patent communication, somewhat drawn out, with the oesophagus; the duct is sharply separate, as long as the ampulla.

Owing to the internal degeneration in the genital segments and the generally unfavourable condition of the worms, I am unable to describe completely the penial body, concerning which Michaelsen has not given us any information. The vas deferens appears to pass backwards in numerous windings for several segments, I think as far as segment xiv; the penial body seems to have possessed a muscular capsule, and not to have consisted of discrete masses of gland cells after the manner of *E. albidus*.

The locality of the specimens deserves a word of note; they were dredged from 160 m.—a very unusual depth for Oligochaetes, which are usually confined to the shore and seldom stray out to sea. Michaelsen's specimens were found with *Marionina georgiana* about low-water mark, in shaly detritus,

among the roots of seaweeds, and in the canal system of sponges. Another species of the genus, *M. macrochaeta* (Bay of Naples, coast of Ireland), lives, like the specimens of the present collection, below low-water mark.

Genus Achaeta, Vejd.

St. MS 71. 9. iii. 26. From moss between Grytviken and Maiviken, East Cumberland Bay, South Georgia. A single specimen; along with *Marionina georgiana*.

The interior of the single specimen was much disorganized, and specific determination was impossible.

The genus is known from Europe and New Zealand, but not hitherto from more southerly regions.

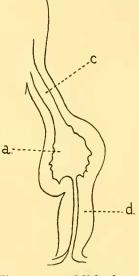


Fig. 14. Michaelsena monochaeta; spermatheca. a. ampulla; c. communication with oesophagus; d. duct.

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